

# Review of the Nearctic species of *Enargia* Hübner, [1821] (Noctuidae, Noctuinae, Xylenini)

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## Abstract

The taxonomy and nomenclature of the Nearctic species of *Enargia* Hübner shows a long history of misunderstood species concepts and misapplied names, and the group is revised here. *Enargia infumata* (Grote, 1874) is a senior synonym of what has been referred to as *E. mephisto* Franclemont, 1939 for the past 70 years. Late summer moths from boreal areas of Canada and northeastern United previously identified as *E. infumata* have no available name and are here described as *E. fausta* **sp. n.** A lectotype for *Orthosia infumata* Grote is designated. Adults and genitalia of the three North American species (*E. infumata*, *E. fausta*, and *E. decolor*) are illustrated, and a diagnostic key is provided.

## Keywords

Aspen two-leaf tier, taxonomy, Cosmiina, Canada, United States, North America, *Populus tremuloides*, defoliator

## Introduction

*Enargia* Hübner, [1821] (subtribe Cosmiina) contains about 13 species worldwide (Poole 1989). Fibiger and Hacker (2007) list eight Palaearctic species, and treat the

two European species in detail. In the Nearctic three species were revised by Franclemont (1939). As such, *Enargia* is a Holarctic genus primarily of temperate zones. A diagnosis of the genus is given by Fibiger and Hacker (2007), who note the following autapomorphies: 1) peniculus (lobe-like extension of the dorsal tegumen) extremely large and consisting of two lobes: a stout lobe at the base of the uncus and a long, rounded-triangular lobe on the subdorsal tegumen, and 2) vesica with two broad-based cornuti, with the apex directed toward the base of the vesica.

In North America, *Enargia decolor* (Walker) has a transcontinental distribution and can reach population levels high enough to cause extensive defoliation of aspen (*Populus tremuloides* Michx.) stands in boreal forests (Wong and Melvin 1976, and references therein). The other two Nearctic species, which have previously gone under the names *E. infumata* (Grote) and *E. mephisto* (Franclemont), apparently do not reach outbreak population levels, although records could possibly be confounded by the difficulty in identifying adults and particularly larvae of all three species, and given the taxonomic issues discussed below. All three species can be quite variable in wing markings, and prior to Franclemont's revision all North American taxa were treated as a single species, although Dod (1905; 1913) recognized that *E. infumata* was distinct from *E. decolor*.

Due to the variability in wing pattern and colour, and inadequate study of diagnostic morphology traits, the two closely-related species previously known as *E. mephisto* and *E. infumata* have been misunderstood. *Enargia infumata* (including *E. mephisto*) is actually more widespread and variable than previously defined, whereas *E. infumata* (of authors) is much more conservative in colour variation and has a narrower more northerly distribution. The confusion of these two taxa is compounded by the fact that the type specimen of *E. infumata* (Grote) is the same species as *E. mephisto* (Franclemont), so *E. infumata* (Grote) is a senior synonym of *E. mephisto*, and *E. infumata* (of authors) has no available name. The purpose of this paper is to rectify this taxonomic issue, and to provide a diagnostic review of the North American *Enargia*.

## Methods and materials

Adult genitalia were prepared following the methods detailed by Lafontaine (2004). Cleaned, stained genitalia were stored and examined in 30% ethanol, and slide-mounted in Euparal before being photographed. Inflated male vesicae were photographed in ethanol prior to being slide-mounted to prevent distortion and ensure consistent viewing angles.

Specimens examined during the course of this study were primarily those of the CNC, UASM, and NOFC. Standard two-letter postal abbreviations for Canadian provinces and U.S. states are used here.

Molecular variation was assessed based on the 658 base-pair 'barcode' region of the first subunit of the cytochrome oxidase (*cox1*) gene (Hebert et al. 2003). DNA was

extracted from one leg removed from a dried specimen, and processed at the Canadian Centre for DNA Barcoding, Guelph, Ontario. DNA extraction, amplification and sequencing protocols for the Barcode of Life initiative are given in Hebert et al. (2003). Barcode haplotypes were compared with phylograms constructed using the neighbour-joining method in PAUP 4.0\*b10 (Altivec) (Swofford 2002). Phyletic distances were calculated using the Kimura-2-Parameter (K2P) distance model. Data for molecular voucher specimens, including trace files and photographs, are available at <http://barcodinglife.com> (project: Lepidoptera of NA Phase II: “*Enargia* revision” under the “Published Projects” tab).

Abbreviations of collections referred to herein are as follows:

<b>AMNH</b>	American Museum of Natural History, New York, New York, USA
<b>BMNH</b>	The Natural History Museum (formerly British Museum [Natural History]), London, UK.
<b>CUIC</b>	Cornell University Collection, Ithaca, New York, USA.
<b>CNC</b>	Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario, Canada
<b>DHC</b>	Daniel Handfield Collection, St-Mathieu-de-Beloeil, Québec, Canada
<b>LHC</b>	Louis Handfield Collection, Mt-St-Hilaire, Québec, Canada.
<b>NOFC</b>	Northern Forestry Centre, Canadian Forest Service, Edmonton, Alberta, Canada.
<b>UASM</b>	University of Alberta Strickland Entomological Museum, Edmonton, Alberta, Alberta, Canada.
<b>USNM</b>	National Museum of Natural History (formerly United States National Museum), Washington, D.C., USA.

## Systematics

### Key to species of Nearctic *Enargia* Hübner

1. Forewing without black spot at base of reniform, at most with basal grey shading, but this never darker than other forewing markings; outline of claviform spot often present as thin dark line below orbicular; break of antemedial line generally pointed, at right angle or slightly greater; male with corona of valve extending along 1/2 of valve length (Figs 55, 56); females with abdomen thinly scaled and longer than that of males, ovipositor usually protruding beyond terminal scales; ductus bursae (appearing as bulbous rugose area separated from corpus bursae) 0.4–0.6 × as long as (sclerotized) segment VIII (Figs 64, 65) ..... *E. decolor*
- Forewing with black spot at base of reniform that is distinctly darker than other forewing markings (Figs 1–33) (may be obscure in very dark specimens, e.g. Figs 1, 16); claviform entirely absent; angle of antemedial line generally rounded, obtuse; male with corona of valve extending along valve

- for 2/3 of valve length; females with abdomen scaled as in male (except for lateral and terminal tufts); abdomen length same as that of male, ovipositor not usually protruding beyond terminal scales; ductus bursae (appearing as bulbous rugose area separated from corpus bursae)  $0.8\text{--}1.0 \times$  as long as (sclerotized) segment VIII (Figs 66, 67) ..... **2**
2. Forewing highly variable in colour, but only rarely yellow ochre with contrasting dark markings (Figs 1–18); AM and PM lines usually indistinct, not thin, sharp, and contrasting; border of reniform and orbicular usually weakly defined and interrupted, or absent altogether; hindwing ground colour dull ochre to greyish ochre; male genitalia with right cornutus relatively small, i.e., length of sclerotized plate  $4\text{--}5 \times$  greater than length of free apex of cornutus (Fig. 59); female corpus bursae  $5\text{--}6 \times$  length of segment VIII, and gradually tapering to terminal sac (Fig. 64) ..... ***E. infumata***
- Forewings yellow ochre to orange ochre with contrasting dark markings (Figs 19–30), never unicolourous grey or brown; AM and PM lines distinct, sharp, and contrasting; border of reniform and orbicular usually sharply defined and continuous; hindwing ground colour yellow ochre; male genitalia with right cornutus relatively large, i.e., length of sclerotized plate only  $2\text{--}2.5 \times$  greater than length of free apex of cornutus (Fig. 60); female corpus bursae  $3.5\text{--}4 \times$  length of segment VIII, with terminal sac abruptly tapered (Fig. 65) ..  
..... ***E. fausta* sp. n.**

***Enargia infumata* (Grote, 1874)**

Figs 1–18, 55, 59, 64.

*Orthosia infumata* Grote, 1874; 160.

*Cosmia punctirena* Smith, 1900; 222, pl. 5, f. 6.

*Cosmia punctirena*; Dod 1905.

*Enargia mephisto* Franclemont, 1939; 115, f. 2, **syn. n.**

*Enargia infumata*; Forbes 1954, in part

*Enargia mephisto*; Rings et al. 1992, pl. XV f. 23. Handfield 1999, p. 92, f. 9551-1, 9551-2.

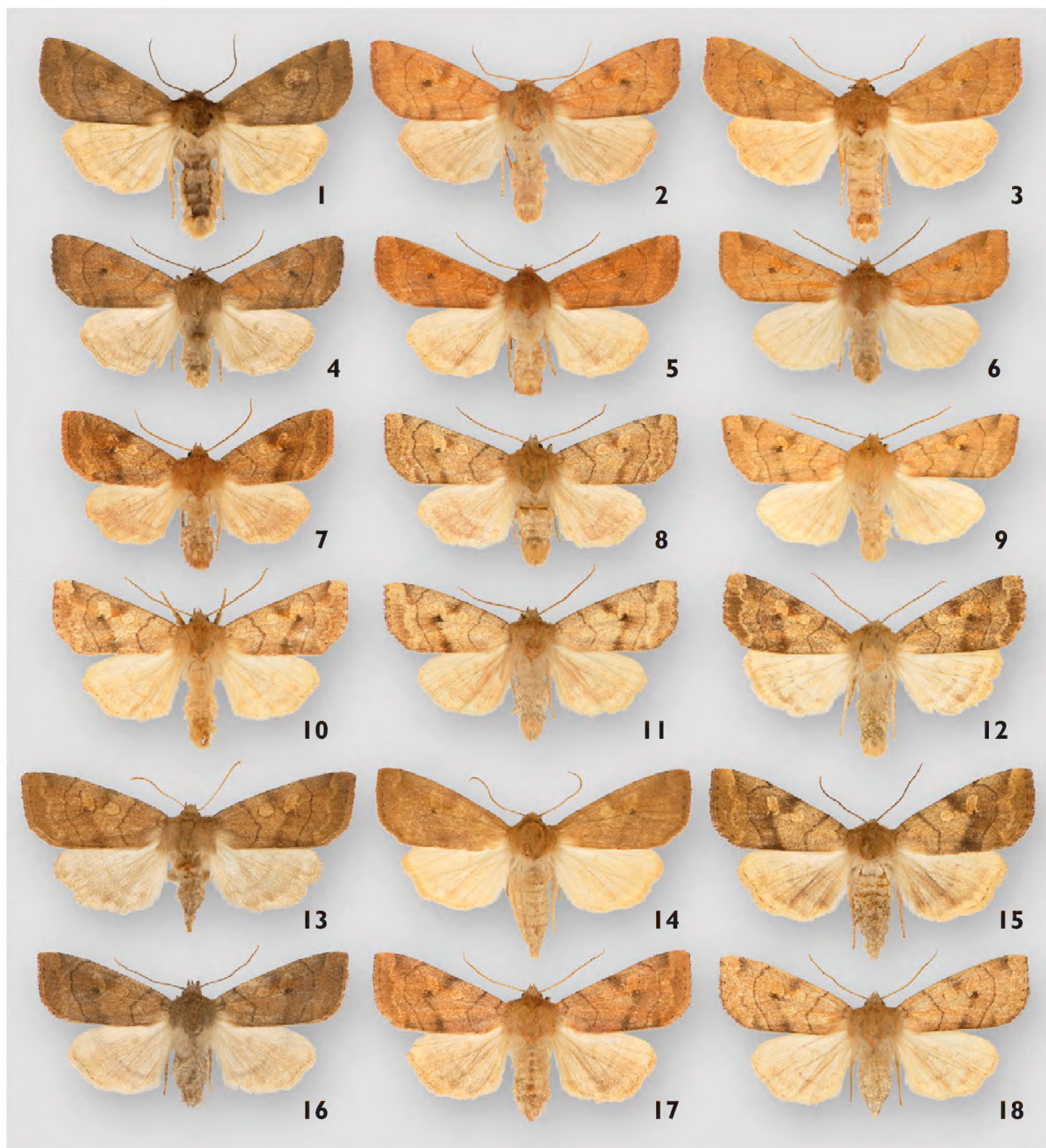
**Type material.** *Orthosia infumata*: **lectotype** female, here designated. BMNH, examined. Type locality: “Chautauqua Co., N. Y.” Although Grote’s (1874) statement in the original description that “specimens received from Mr. Geo. Norman” suggests that *E. infumata* could have been based on several syntypes, only one wing expanse measurement is given, and the type locality is restricted to Chautauqua Co., NY. Norman’s material originates from Ontario (M. Honey, pers. comm.). The type material most likely was a single Chautauqua Co. specimen, although this is not beyond question. To ensure the stability of the name *Orthosia infumata*, the following female specimen is therefore designated as **lectotype**: “Grote Coll.”; “U.S. America / [crossed out,

undecipherable] Co. / Chautauqua / Co. / N.Y.”; “1938. / 265”; “Type” [round, red bordered label]; *Orthosia* / *infumata* / Type Grote” [BMNH]. The following label will be added: “*Orthosia* / *infumata* Grote / Lectotype by / Schmidt, 2010”. Although the abdomen is missing, the specimen is otherwise in good condition, and shows the dusky grey-ochre forewing colour (probably reflected by the name *infumata*) with a poorly contrasting reniform and orbicular, less sinuate AM line, dull ochre hindwing, and smaller wing expanse compared to the species previously thought to be *E. infumata* and described here as *E. fausta*.

*Cosmia punctirena*: **lectotype** male (designated by Todd 1982). USNM, photograph examined. Type locality: “Yellowstone Park, Wyoming.” The specimen illustrated by Smith (1900) is the lectotype designated by Todd (1982), and the relatively unicolourous, dark forewing, non-contrasting reniform and orbicular, and pronounced black spot in the reniform, show that *E. punctirena* is correctly attributed to the synonymy of *E. infumata*. Additional Barnes specimens collected in August in Yellowstone (CNC) are of the same provenance as the original types, although these are not paralectotypes, and are also *E. infumata*. The original description of *E. punctirena* was probably based on a mixed series of *E. infumata* and *E. decolor*, as *E. decolor* specimens in the CNC from Glenwood Springs, Colorado (Barnes, September) and *E. decolor* from Cartwright, MB (Heath, August) are of the same provenance as the original syntype series. Although this does not affect the synonymy of *punctirena*, the diagnosis of the taxon by Smith is inaccurate.

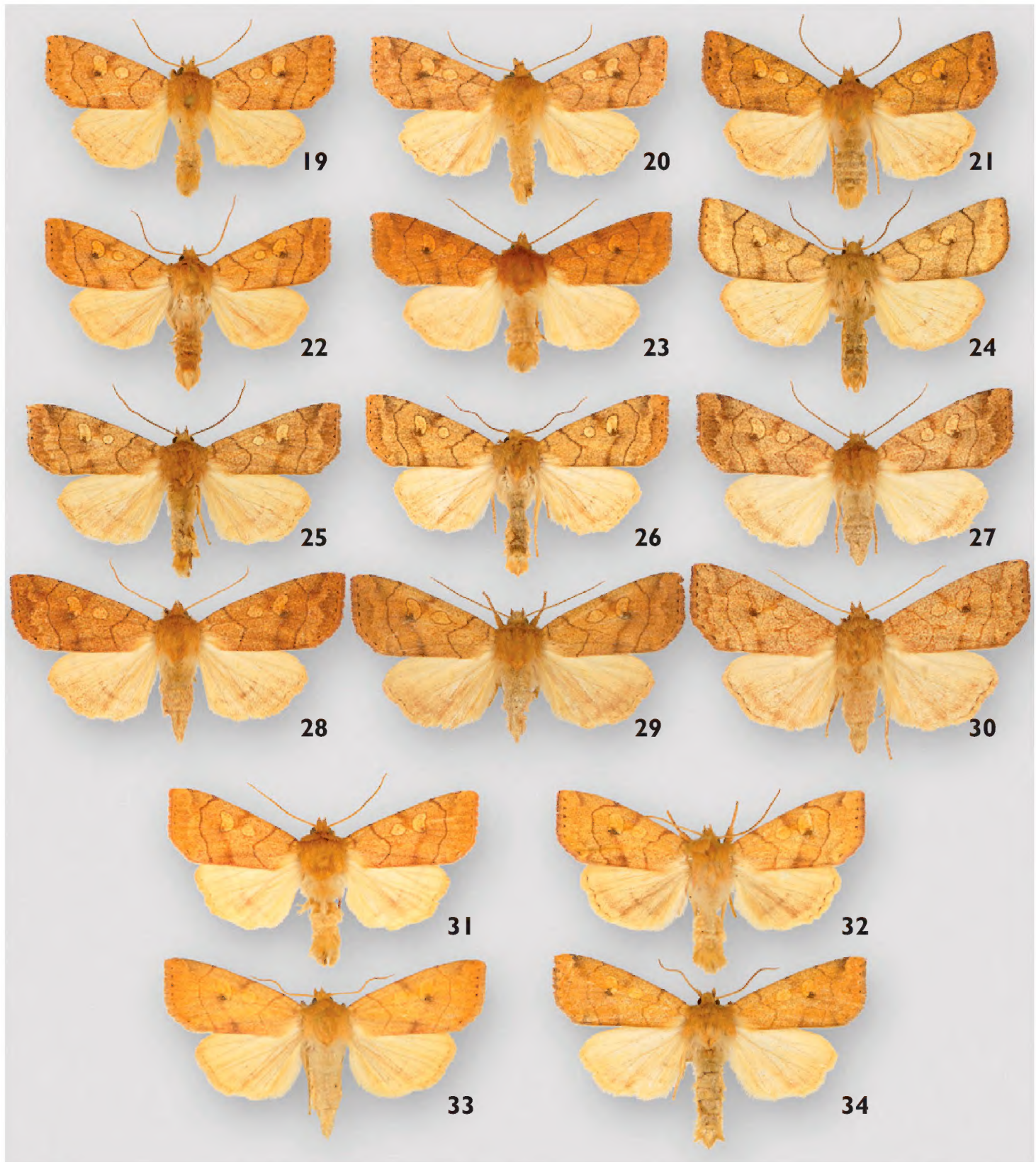
*Enargia mephisto*: **holotype** male. CUIC, examined. Type locality: “Ithaca, New York.” see ‘Remarks’ below.

**Diagnosis.** *Enargia infumata* is most similar to *E. fausta*. Overall, *E. infumata* has a paler ochre, less yellow look to it with less contrasting markings and greater variation in colour. The unicolorous smoky-grey forms are unique to *E. infumata* (it was this phenotype that formed the basis of Franclemont’s description of *E. mephisto*). Compared to *E. fausta*, *E. infumata* is slightly smaller, has slightly thicker, less sharply defined AM and PM lines (when these are visible at all), less sinuate PM line, a dull, pale ochre (vs. yellow-ochre) hindwing ground colour, and the reniform and orbicular are often concolourous with the forewing ground colour (not paler and contrasting), and with a discontinuous or absent outline (thin, crisp outline in *E. fausta*). Specimens of *E. infumata* from the Prairie Provinces average slightly larger and paler than eastern *E. infumata*, and therefore have a general appearance more like that of *E. fausta*. Internally, the valve length is shorter in *E. infumata* (2.6–2.9 mm from apex to clasper at dorsal margin, vs. 3.3–3.5 mm in *E. fausta*), the cornuti of the vesica are smaller overall (length of free apex less than 0.10 mm vs. greater than 0.11 mm in *E. fausta*), with a relatively much larger sclerotized plate of the right cornutus (length of plate 4–5 × greater than length of free apex of cornutus, compared to 2.0–2.5 × in *E. fausta*). The peniculum (tegumen lobes) are on average shorter and broader (Franclemont 1939; Forbes 1954), but there is much overlap in shape between the two species and this is not a reliable diagnostic trait. In the female, the corpus bursae differs in size and shape, being longer (5–6 × length of segment VIII vs. 3.5–4.0 × in *E. fausta*), and more narrow-elongate than *E. fausta* (Fig. 64).



**Figures 1–18.** *Enargia infumata* adults. **1–3** ♂, Kootenay Plains, AB, CAN **4–11** ♂, Edmunston, NB, CAN **12** ♂, Taber, AB, CAN **13** ♀, Panguitch, UT, USA **14–15** ♀, Kootenay Plains, AB, CAN **16–18** ♀, Edmunston, NB, CAN.

**Redescription.** *Head* – Antenna of male prismatic, segments as wide as long; antenna of female filiform and ciliate; scales of dorsal antenna, scape, vertex, and palpus unicolorous but co-varying with ground colour of wings, from pale ochre, yellow ochre, brownish grey, to dull rusty brown. *Thorax* – Vestiture of thorax, patagia and prothoracic collar unicolorous, but varying from pale ochre, yellow ochre, brownish grey, to dull rusty brown; legs dull ochre yellow with longer scales of corresponding colour on femur and tibia. *Wings* – Forewing length: eastern populations average slightly smaller at 16.4 mm (n = 6) versus 17.4 mm (n = 6) for western populations; females slightly larger overall at 17.5 mm (n = 3) for eastern and 18.4 mm (n = 3) for western

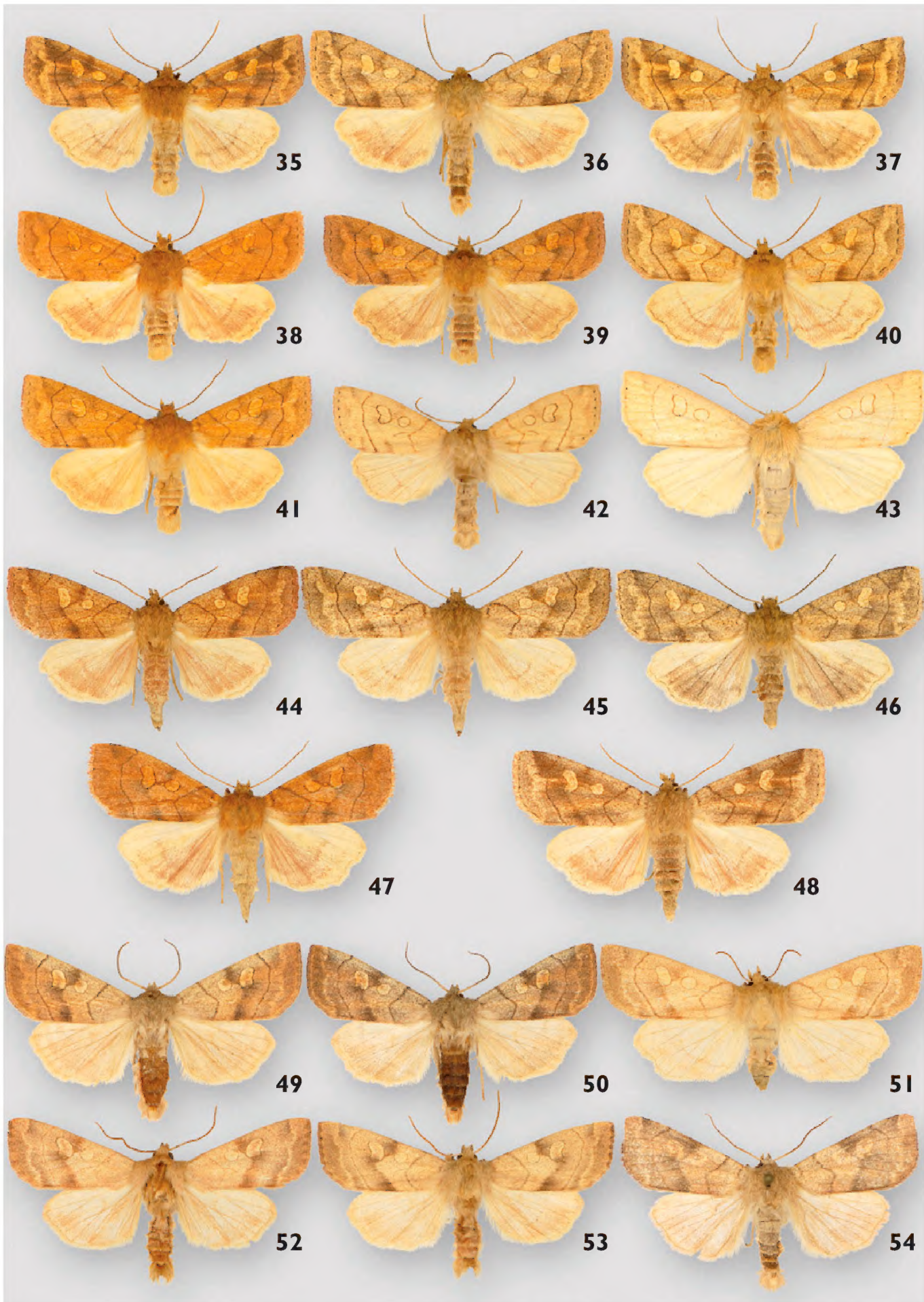


**Figures 19–34.** *Enargia* adults. **19** *E. fausta*, holotype ♂, St.-Basile, NB, CAN **20** *E. fausta*, ♂, Edmunston, NB, CAN **21** *E. fausta*, ♂, Temiscouata Co., QC, CAN **22** *E. fausta*, ♂, Black Sturgeon L., ON, CAN **23** *E. fausta*, ♂, Edmunston, NB, CAN **24** *E. fausta*, ♂, Peers, AB, CAN **25** *E. fausta*, ♂, Edmunston, NB, CAN **26** *E. fausta*, ♂, Black Sturgeon L., ON, CAN **27** *E. fausta*, ♀, St.-Basile, NB, CAN **28–30** *E. fausta*, ♀, St.-Basile, NB, CAN **31** *E. ?paleacea*, Delta, BC, CAN **32** *E. paleacea*, ♂, Hungary **33** *E. paleacea*, ♀, Hungary **34** *E. paleacea*, ♂, Finland.

specimens; forewing ground color varying from pale ochre, yellowish ochre, brownish grey to rusty brown; dark markings varying from charcoal grey to reddish brown, and highly contrasting to virtually absent; angle of antemedial line rounded and obtuse, about 130°–140°; postmedial line evenly rounded to slightly sinuate; medial band varying from thick and diffuse to obsolete, co-varying with dark terminal and sub-

apical shading; pale subterminal line present in specimens with dark terminal shading (Fig. 12); reniform and orbicular usually concolorous with wing ground colour or only slightly paler, rarely contrastingly pale; border of reniform and orbicular weakly defined and usually interrupted, or absent altogether; base of reniform (towards anal margin) with dark grey spot of varying size, but spot nearly always darkest of forewing markings; claviform absent; fringe concolorous with ground colour; ventral forewing less variable than dorsum, ground colour pale yellowish ochre with postmedial line and reniform spot variously developed, more so in specimens with contrasting dorsal markings and antemedial line absent. Hindwing ground colour pale yellowish ochre with dark shading varying in extent and colour from grey to dull maroon; postmedial line and broader, diffuse subterminal band visible when dark markings developed, varying to entirely absent; medial line better defined ventrally, with ventral discal spot similarly dark (rarely visible dorsally). *Abdomen* – Vestiture mix of pale yellowish-ochre and darker scales of colour of those on forewing dark markings; males with terminal and lateral scale tufts, which are absent in females. *Male genitalia* – (Figs 55, 59). Uncus cylindrical, tapering to a small distal hook; tegumen with large peniculus, consisting of long, triangular subdorsal lobe,  $0.3 \times$  length of valve, and short, rounded lobe adjacent to uncus base; valve 2.6–2.9 mm long,  $4 \times$  as long as wide (measured at widest part), corona extending from apex along ventral margin over  $1/2$  length of valve; sacculus  $0.5 \times$  valve length; clasper spatulate, recurved, and directed caudally; aedeagus  $7 \times$  as long as wide, tube shaped, with field of 10–18 short, stout backward-directed spines at ventral margin of apex; ventral margin of apex rounded and slightly scoop-like; vesica small, simple, bulbous,  $0.4 \times$  length of aedeagus, with two stout cornuti positioned laterally and directed caudad; free apex of cornuti equally sized (0.082–0.099 mm); distal opening of vesica extending dorsally from vesica as gradually tapering tube. *Female genitalia* – (Fig. 64). Ovipositor lobes bluntly triangular in lateral view, ventral margin slightly concave, covered in short hair-like setae; abdominal segment VIII  $0.7 \times$  as long as wide, anterior apophysis  $1.5 \times$  and posterior apophysis  $2.3 \times$  length of abdominal segment VIII; ductus bursae extremely short,  $2 \times$  length of ostium, appearing thicker and more rugose than corpus bursae; long, duct-like proximal two-thirds of corpus bursae (which initially appears to be ductus bursae) with only slight widening toward ovoid distal chamber; corpus bursae  $5\text{--}6 \times$  length of segment VIII, lacking signa; ductus seminalis originating dorsad and slightly caudad of distal end of ductus bursae.

**Distribution and biology.** *Enargia infumata* has a broad North American distribution, occurring from Alaska south to California and the Pinaleno Mountains of Arizona, east to New Brunswick and New York. No specimens were seen from Nova Scotia although the species undoubtedly occurs there; the Nova Scotia specimen illustrated by Ferguson (1954: pl. x, fig. 4) is *E. fausta*. In the eastern part of the range, the peak flight period occurs between mid- and late July, with extreme dates from mid-June to mid-August. *Enargia infumata* flies three to four weeks earlier than *E. fausta*, and there is very little temporal overlap between the two in any given year; generally, *E. fausta* does not appear until late July and peaks in mid- to late August. Flight times for the boreal forest region from northern Ontario westward indicate slightly later



**Figures 35–54.** *Enargia* adults. **35** *E. decolor*, ♂, Temiscouata Co., QC, CAN **36** *E. decolor*, ♂, Princeton, BC, CAN **37–38** *E. decolor*, ♂, St.-Basile, NB, CAN **39–41** *E. decolor*, ♂, Edmundston, NB, CAN **42** *E. decolor*, ♂, Wainwright sand dunes, AB, CAN **43** *E. decolor*, ♀, Josephine, OR, USA **44** *E. decolor*, ♀, Hanwell, NB, CAN **45–48** *E. decolor*, ♀, Edmundston NB, CAN **49** *E. decolor*, ♂, Dalton Springs cmpgd., San Juan Co., UT, USA **50** *E. decolor*, ♂, Dalton Springs cmpgd., San Juan Co., UT, USA **51** *E. decolor*, ♀, Chiloquin, OR, USA **52** *E. decolor*, ♂, McGill, NV, USA **53** *E. decolor*, ♂, Durango, CO, USA **54** *E. decolor*, ♂, Mt. Graham, Graham, Co., USA.

flight dates for *E. infumata*: In central Alberta, *E. infumata* peaks from late July to mid August, with *E. fausta* again slightly later in mid- to late August.

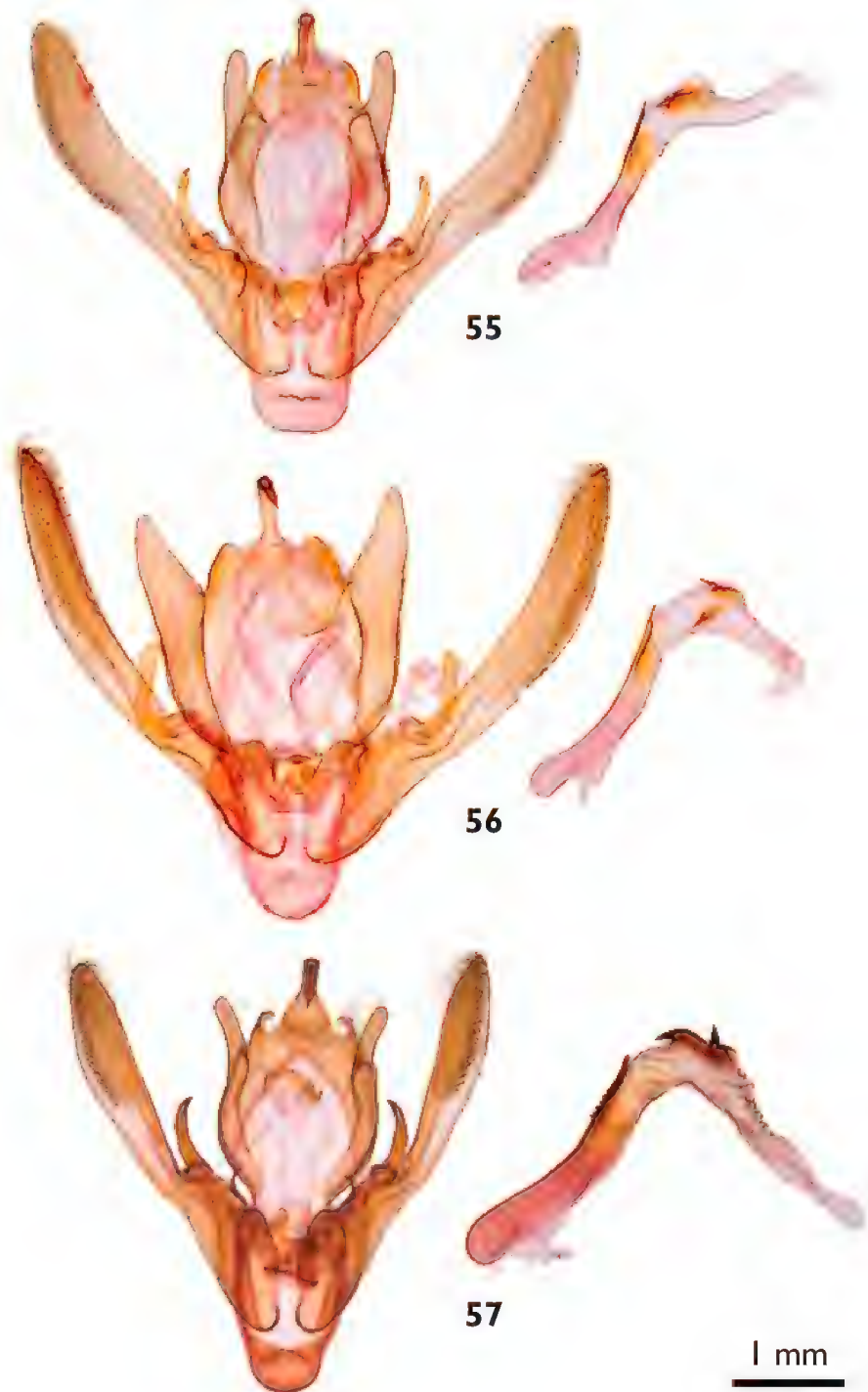
McGuffin (1958) illustrates the larval head capsule and provides a detailed description identified as *E. infumata*, but given the past confusion of *E. infumata* and *E. fausta*, it is not certain which species his account pertains to. I have not been able to find vouchers or associated adults in McGuffin's material at the CNC. Prentice (1962) reports most larval collections (45/61) from *Populus tremuloides* Michx., some from *Betula papyrifera* Marsh. (13/61) and a few collections from *Salix* sp. (2 collections) and *Populus balsamifera* L. (1 collection), but again it is not clear if these records pertain to *E. infumata* or *E. fausta*, but likely both, since *E. mephisto* is not mentioned in Prentice (1962). I have confirmed *P. tremuloides* as a definite (and probably preferred) host from reared specimens. The larval biology and description needs to be re-evaluated.

**Remarks.** Franclemont (1939) correctly recognized that three species were going under what had previously been treated as a single species, *E. decolor*. Dod (1905) also recognized early on that *E. decolor* and *E. infumata* were separate species, and gave several diagnostic traits separating the two (which I had initially overlooked, and Franclemont (1939) made no mention of either). Franclemont (1939) recognized a third species and described it as *E. mephisto*, based on two specimens. Comparison of phenotype and genitalic variation in long series of *E. mephisto* and *E. infumata* (of authors), and *COI* sequence data shows that these two taxa have been largely misunderstood. Variation in the size and shape of the tegumen arms ('shoulders' of Franclemont) shows that these characters are not diagnostic, and the most consistent male genitalic character is the size and position of the cornuti of the inflated vesica (Fig. 59) (Franclemont used uninflated vesicae in his diagnosis). Additional distinguishing characters are given under 'Diagnosis,' above.

Why Franclemont considered all of the other 81 specimens from sites across the continent to be *E. infumata* (of authors; = *fausta*) rather than *E. mephisto* is not clear, since many western specimens are indistinguishable from eastern *E. mephisto* (compare Figs 1, 13, 16). Presumably he had few western specimens and lacked the 'typical' *E. mephisto* phenotype in his material, compounded by the slightly larger, paler western phenotype of *E. infumata* (Grote), which therefore bears greater resemblance to *E. fausta*. It would therefore have been difficult to 'draw the line' between *E. fausta* and phenotypic variation in *E. mephisto* without long series of specimens and extensive comparison of dissections.

Following Franclemont's revision, the more northerly pale species described herein as *E. fausta* and the paler forms of the widespread species *E. infumata* were both treated as *E. infumata*, whereas the darker forms of *E. infumata* were treated as *E. mephisto*. *Enargia infumata* (as *E. mephisto*) was thought to be the less common taxon with a more easterly distribution (Forbes 1954). In reality *Enargia infumata* s.s. is widespread and common, whereas *E. fausta* has a more restricted distribution.

The seventeen sequenced specimens of *E. infumata* from British Columbia, Alberta, Ontario, and New Brunswick exhibited seven haplotypes, differing at most by approximately 0.6 % from each other, compared to a 1.7% divergence from the single *E. fausta* specimen.



**Figures 55–57.** Male genitalia of *Enargia*. **55** *E. infumata* **56** *E. fausta* **57** *E. decolor*.

***Enargia fausta* Schmidt, sp. n.**

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Figs 19–30, 56, 60, 65

*Enargia infumata* Franclemont 1939, in part; Handfield 1999: p. 92 f. 9550; Rockburne and Lafontaine 1976: f. 434; Ferguson 1954: pl. X f. 4.

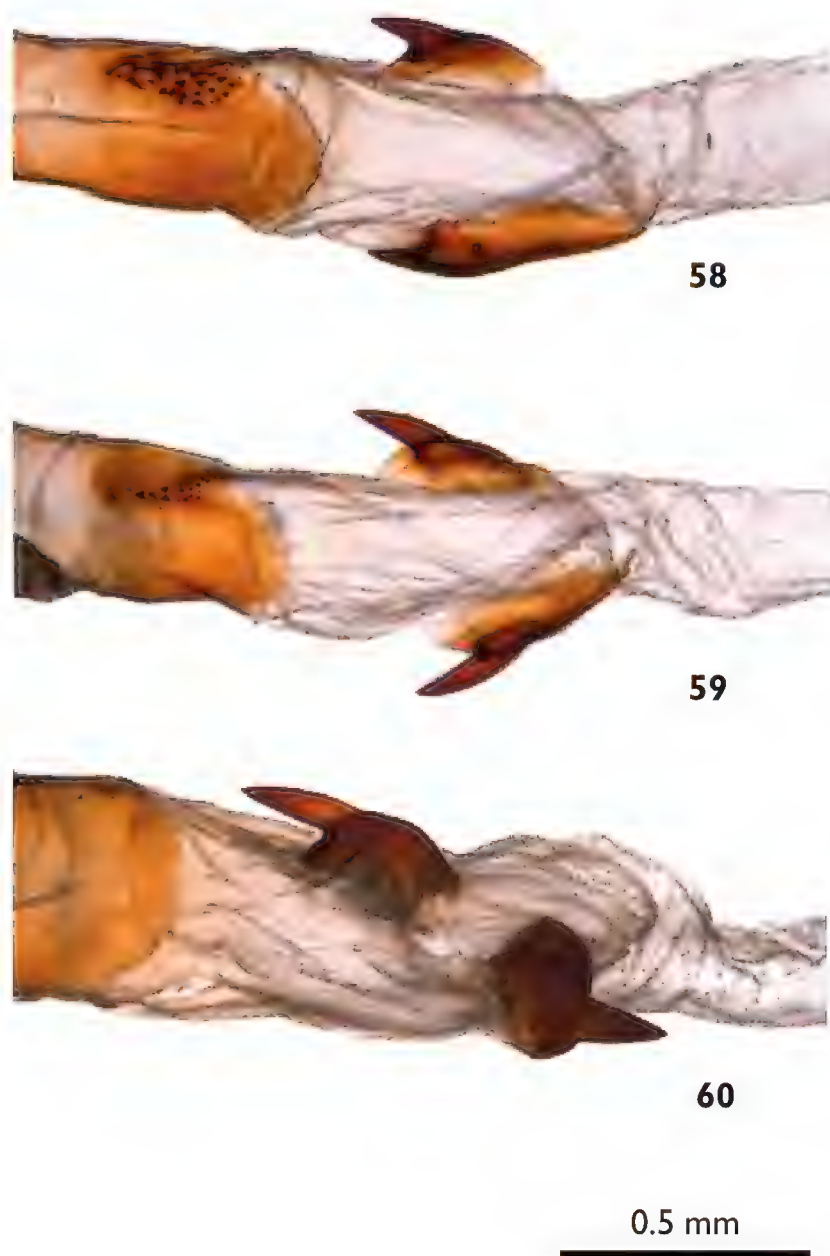
**Type material. Holotype** ♂. St.-Basile, N. B. [New Brunswick] / Canada. 14. VIII. 1994 / leg. Henry Hensel “HOLOTYPE / *Enargia fausta* / Schmidt, 2010” [red typed label] [CNC]. **Paratypes:** 55 ♂, 49 ♀ (CNC, UASM, DHC, LHC). **New Brunswick.** Same data as holotype, 19 Aug 1993 (1 ♀); Edmunston, 31 Aug 1991 (1 ♂), 16 Aug

2002 (1 ♂), 8 Aug 2003 (1 ♀), 20 Aug 2003 (4 ♂, 3 ♀), 17 Aug 2003 (1 ♂, 1 ♀), 21 Aug 2003 (1 ♂), 27 Aug 2003 (1 ♀), 25 Aug 2003 (1 ♀), H. Hensel; Hanwell, 14 Aug 2007, G. Hensel (1 ♂). **Quebec.** Temiscouata Co., 18 Aug 1992, H. Hensel (1 ♂); Lac Mondor, Ste. Flore, 27 Jul 1951, E.G. Munroe (1 ♂); Laniel, 23 Aug 1932 (2 ♂, 2 ♀), 24 Aug 1932 (1 ♂), 26 Aug 1932 (1 ♀), W.J. Brown; Forestville, 11 Aug 1950 (2 ♂), R. de Ruelle; Belisle Beach, Luskville, 12–19 Aug 1961, E.G. Munroe (1 ♂); La Présentation, 5 Aug 1971, L. Handfield (2 ♂); Mont-Saint-Hilaire (Chemin des Lots), 3 Sep 1971, L. Handfield (1 ♀); Mont-Saint-Hilaire (Manoir Rouville-Campbell), 20 Aug 1969 (1 ♀), 23 Aug 1969 (1 ♀), 26 Aug 1968 (1 ♀), 29 Aug 1969 (1 ♀), 30 Aug 1971 (1 ♂, 4 ♀), 31 Aug 1971 (1 ♀), 2 Sep 1971 (9 ♀), L. Handfield; Mont-Saint-Hilaire (Rang des Étangs), 21 Aug 1978 (1 ♂, 1 ♀), L. Handfield; Saint-Valérien, comté de Rimouski, I. Blais, 21 Aug 1971 (1 ♀), L. Handfield; St-Michel des Saints, Lac Dussault, 8 Aug 2005, D. Handfield, barcode voucher DH010701, (1 ♂); Terrebonne High, 13 Aug 1938 (1 ♀), 3 Aug 1941 (1 ♂), L. Auger. **Ontario.** Thunder Bay Co., Inwood Prov. Park nr. Upsala, 10 Aug 1982, J.F. Landry; Black Sturgeon Lake, 3 Aug 1964 (1 ♂, 1 ♀), 14 Aug 1963 (1 ♂, ♀), 2 Sep 1964 (1 ♂), 28 Aug 1964 (2 ♂), 21 Aug 1963 (1 ♂); Thunder Bay, Stanley Area, 12 Aug 1980 (1 ♂), J. P. Wales; La Passe, 16 Aug 1974 (1 ♂), E.W. Rockburne; Biscotasing, 16 Aug 1931 (1 ♂), 29 Jul 1931 (1 ♂), 30 Aug 1931 (1 ♂), K. Schedl; Ogoki, 14 Aug 1952 (2 ♂), 19 Aug 1952 (10 ♂, 7 ♀), 15 Aug 1952 (2 ♀), 21 Aug 1952 (1 ♀), 16 Aug 1952 (3 ♂); Mississagi Is., North Channel, 7 Aug 1977 (1 ♂), J.K. Morton. **Michigan.** Sault St. Marie, 27 Aug 1960, (1 ♂), Kelton & Whitney. **Alberta.** Peers, 4 mi. N, 2650', 26 Jul 1961, D.F. Hardwick (1 ♂); Edmonton, 2 Aug 1942, K. Bowman, UASM14971, (1 ♂); Heart Valley, (no date), reared ex *Populus tremuloides*, (1 ♀); Wembley, 1954, reared ex *Populus tremuloides*, (1 ♂ 1 ♀); Overflow, (no date), reared ex *Populus balsamifera* (1 ♂, stunted); Rocky Lake, 1957, reared ex *Betula papyrifera* (2 ♀).

**Diagnosis.** Similar to and long confused with *E. infumata*, see diagnosis under that species.

**Etymology.** The specific epithet is derived from Faustus, the alchemist of German legend who sold his soul to Mephistopheles, or Mephisto, in exchange for knowledge. The ending is amended for a more euphonious combination with *Enargia*, and is a noun in apposition.

**Description.** *Head and thorax* – Colour ranging from pale ochre, yellow ochre, to rusty orange yellow, otherwise not differing from that of *E. infumata*. *Wings* – Forewing length: males 17.5 mm (n = 6), females slightly larger overall at 19.4 mm (n = 5); forewing ground color varying from yellowish ochre to rusty ochre, but not exhibiting the very pale ochre or greyish phenotypes observed in *E. infumata*; dark markings varying from charcoal grey to brownish grey, usually highly contrasting and sharply defined; angle of antemedial line rounded and obtuse, but less so than in *E. infumata*, averaging 110°–120°; postmedial line evenly slightly sinuate medially, only rarely evenly rounded; medial band moderately to poorly developed, co-varying with dark terminal and subapical shading but without the variation extremes seen in *E. infumata*; pale subterminal line present in specimens with dark terminal shading (Figs 12, 15); reni-



**Figures 58–60.** Comparison of male vesica cornuti in *Enargia* species. **58** *E. infumata* **59** *E. fausta* **60** *E. decolor*.

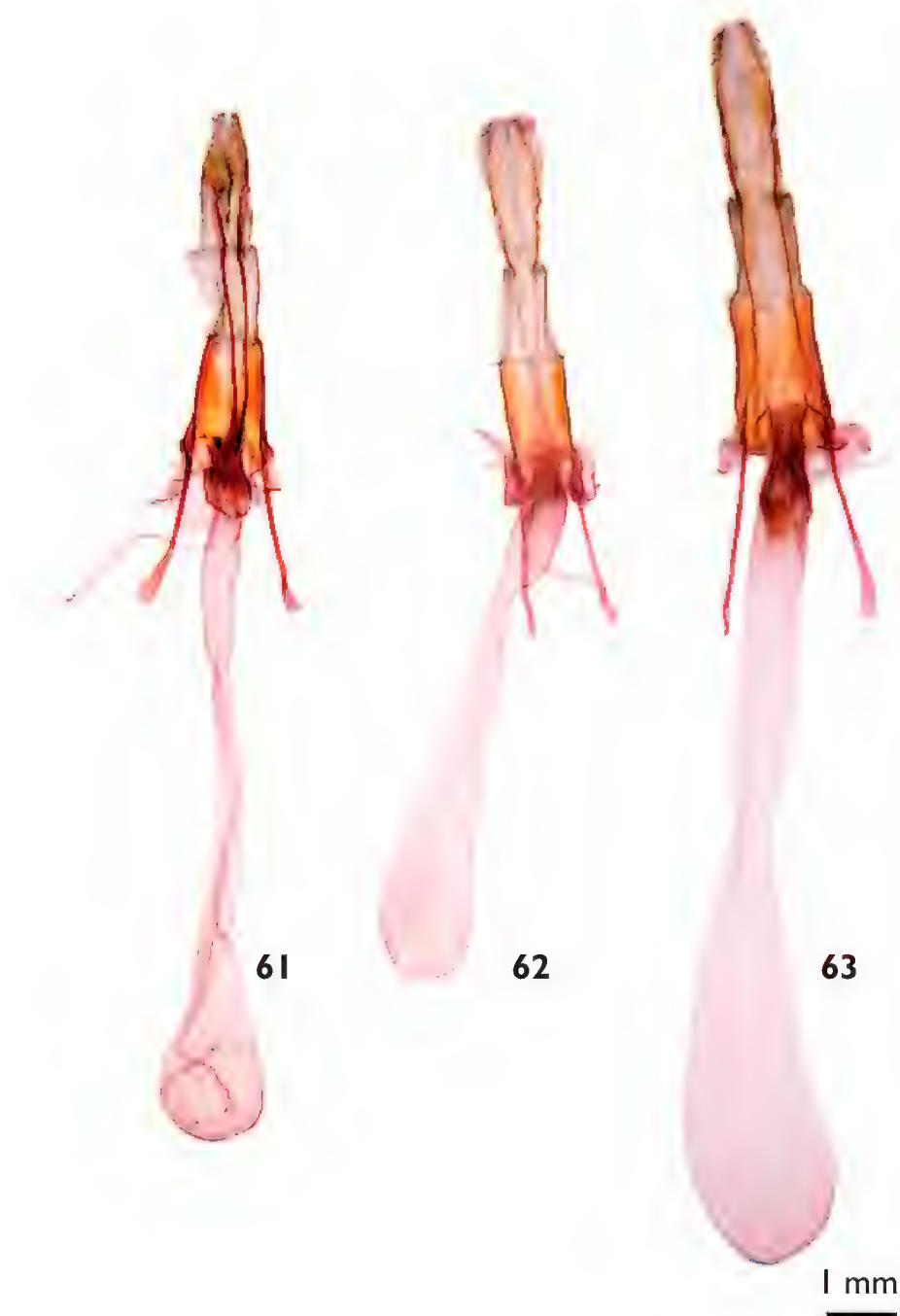
form and orbicular usually paler than ground colour, rarely concolorous; reniform and orbicular with sharply defined, uninterrupted border; base of reniform (toward anal margin) with dark grey spot of varying size, but spot nearly always darkest of forewing markings; fringe concolorous with ground colour; ventral forewing less variable than dorsum, ground colour pale yellowish ochre with postmedial line and reniform spot variously developed, more so in specimens with contrasting dorsal markings, and antemedial line absent. Hindwing ground colour pale yellowish ochre with maroon-grey dark shading of varying extent, but not as grey or extensive as variants of *E. infumata*; postmedial line and broader, diffuse subterminal band visible when dark markings developed, varying to entirely absent; medial line better defined ventrally, with ventral discal spot similarly dark (rarely visible dorsally). *Abdomen* – not differing from that of *E. infumata*. *Male genitalia* – (Figs 56, 60). As for *E. infumata*, but differing in following characters: valve length 3.3–3.5 mm; vesica with free apex of both cornuti equal

in size to each other, ranging from 0.11–0.15 mm; right cornutus small, i.e., length of sclerotized plate of right cornutus only 2.0–2.5 × greater than length of free apex of cornutus (Fig. 60). *Female genitalia* – (Fig. 65). As for *E. infumata*, but differing in size and shape of corpus bursae, in that basal duct-like part shorter and more poorly defined, with a more gradual widening toward apical sac-like chamber; corpus bursae 3.5–4.0 × length of segment VIII.

**Distribution and biology.** *Enargia fausta* has a narrower distribution than *E. infumata* and is essentially restricted to the boreal forest and boreal-deciduous forest transition zone, and unlike *E. infumata* does not range south along the Rocky Mountains nor as far north. Specimens examined range from central Alberta to New Brunswick (but see also Remarks, below) and in the East as far south as the Ottawa River Valley, but the species presumably also occurs in appropriate habitats in northern New York and New England; Ferguson (1954) illustrates a specimen from Glennville, Nova Scotia. Reports of this species from northeastern Ohio (Rings et al. 1992, as *E. infumata*) need to be verified. Flight dates range from late July to early September with most records after mid-August. As discussed under *E. infumata*, the peak flight of *E. fausta* is three to four weeks later than that of *E. infumata*. Available records indicate that this species is much less common than *E. infumata*. It appears that the preferred larval host is white birch (*Betula papyrifera* Marsh.) based on specimens reared from larval collections by the Forest Insect and Disease Survey (NOFC), and also trembling aspen (*Populus tremuloides* Michx.), with a single stunted specimen reared from balsam poplar, *Populus balsamifera* L.. A preference for birch would explain the narrower habitat preference, more restricted range, and lower abundance of this species compared to *E. decolor* and *E. infumata*, both associated with aspen.

**Remarks.** The taxonomic status of an *Enargia* species in the Pacific Northwest (PNW) (Fig. 31) remains unresolved; structurally, they are indistinguishable from boreal *E. fausta*, but externally they are more similar to the European *E. paleacea* (Esper, 1788), with more evenly coloured, orange-yellow forewings (Figs 32–34). *E. paleacea* and *E. fausta* differ in phenotype and DNA barcode divergence, but I have not been able to find genitalic differences. The fact that the PNW specimens are phenotypically most similar to *E. paleacea*, and the large apparent range disjunction of these populations from *E. fausta* (which is not known from central or eastern British Columbia), suggests that the PNW taxon could be a Eurasian introduction via the Vancouver area shipping ports. Alternatively, it could be a coastal segregate of *E. infumata*, or a native Nearctic population of a Holarctic, trans-Beringian *E. paleacea*. However, *E. paleacea* is not known from eastern Siberia, Yukon, or Alaska. It seems most likely that the PNW species represents an accidental introduction of *E. paleacea*, but more research is needed, and DNA sequencing particularly would help to elucidate the taxonomy of these interesting populations.

The single specimen of *E. fausta* for which DNA barcode sequence is available differed by a minimum of 1.7% from *E. infumata* haplotypes. An additional sequenced specimen *E. fausta* (D. Handfield collection, voucher # DH010701), confirmed by dissection, exhibited an *E. infumata* haplotype, suggesting the two species may share haplotypes and that barcodes may not reliably distinguish the two; this requires further study.



**Figures 61–63.** Female genitalia of *Enargia*. **61** *E. infumata* **62** *E. fausta* **63** *E. decolor*.

***Enargia decolor* (Walker, 1858)**

Figs 35–54, 57, 60, 63

*Mythimna decolor* Walker, 1858: 1658.

*Enargia discolor*; Smith 1900; misspelling.

*Cosmia discolor*; Dod 1905; Dod 1910; misspelling.

*Enargia decolor*; Franclemont 1939.

*Enargia decolora*; Hampson 1910: 239; unjustified emendation.

‡*Enargia decolora* ab. *mia* Strand, 1916: 164; unavailable infrasubspecific name.

‡*Enargia decolora* ab. *sia* Strand, 1916: 164; unavailable infrasubspecific name.

**Type material.** *Mythimna decolor*: male **holotype**. BMNH, examined. Type locality: “Orilla [*sic*], West Canada” [Orillia, Ontario, Canada].

**Diagnosis.** *Enargia decolor* is externally most similar to and broadly sympatric with *E. infumata*. Specimens with little dark shading can also be similar to *E. fausta*, particularly females of both species. About 90% of *E. decolor* specimens can be recognized by one or more of the following external characters: reniform spot lacking pronounced dark scaling at base, or if dark scaling present, not darker than color of adjacent medial line; claviform often present as dark dash; well-marked specimens with pronounced hindwing medial line; male antenna slightly serrate, not prismatic. Internally, in males the corona extends only halfway along the ventral margin of the valve ( $2/3$  in *E. infumata* and *E. fausta*, Figs 55, 56), and the vesica cornuti and aedeagus are larger (compare Fig. 60 to Figs 58 and 59). Females have a longer ovipositor and corpus bursae (Fig. 63).

**Distribution and biology.** *Enargia decolor* has a boreal-transcontinental distribution, occurring across the Canadian boreal plain and then southward through the western cordillera at higher elevations, where it is presumably limited by the availability of trembling aspen and possibly other poplars. Records for examined specimens range from northernmost British Columbia (Ft. Nelson) and south-western Northwest Territories (Ft. Smith) east to New Brunswick; also reported from Nova Scotia (Ferguson 1954), Ohio (Rings et al. 1992) and New York (Forbes 1954). In the western United States, specimens were examined from western Montana, Idaho, Washington, Oregon, Nevada, Utah, Wyoming (Albany and Carbon counties), western Colorado, New Mexico (Grant Co.), and Arizona (Graham Co.). Notably, I have not seen any specimens from the Rocky Mountain front ranges of Colorado, where it would be expected to be widespread if there is a continuous distribution southward into New Mexico / Arizona. As discussed under Remarks, the populations from west of the Rocky Mountains south to New Mexico / Arizona may represent a distinct species.

The larvae prefer *Populus tremuloides*, and Prentice (1962) also reported a small number of larval collections from *Betula papyrifera*, *Populus balsamifera*, *Salix* sp., *Populus grandidentata* Michx. and *Alnus rugosa* (Ait.) Pursh. Since this species has mostly been correctly identified, Prentice's larval host records are also probably mostly correct. Larvae can reach high population densities, causing local defoliation of *P. tremuloides* (Wong and Melvin 1976). The balsam poplar group have quite resinous buds and leaves at bud break, so these may not be suitable hosts, at least for early instar larvae. McGuffin (1958) gives detailed descriptions including setal maps of *E. decolor*, but a diagnostic comparison of morphology and biology of larvae to *E. infumata* and *E. fausta* is still needed. Wong and Melvin (1974) describe the larvae and larval biology of *E. decolor*.

**Remarks.** *Enargia decolor* as it is currently defined may consist of two species. Specimens from Nevada, Utah, western Colorado, Arizona and New Mexico are on average duskier, and the medial area tends to be the darkest forewing area (subterminal area equally dark in boreal *E. decolor*); specimens have the markings more obscure overall, often with a pinkish tinge not seen in boreal *decolor*. Comparison of male genitalia from this region to boreal *decolor* also suggest a slight difference. Five bar-coded specimens from Alberta and New Brunswick exhibited four haplotypes, with a

maximum divergence of about 0.26 %; three Utah specimens representing two haplotypes differed between 0.86–1.37 % from the Alberta / New Brunswick material. Additional specimens from key geographic areas (Colorado, Wyoming, Idaho, Oregon) are needed to fully evaluate the taxonomic status of these populations.

## Discussion

The North American *Enargia* species fall into two groups, the *decolor* group and the *infumata* group; the *decolor* group currently includes only *E. decolor*, and possibly an unrecognized species (See ‘Remarks’ under *E. decolor*). *Enargia infumata* and *E. fausta* make up the *infumata* group; *E. fausta* appears to be most closely related to the Eurasian *E. paleacea*. Poole (1989) lists 13 species in *Enargia* globally, although *E. ypsillon* has subsequently been transferred to the genus *Apterogenum* Berio, 2002, and with two additional Palearctic species listed by Fibiger and Hacker (2007). The only European species closely related to the North American group is *E. paleacea*. A cursory examination of the remaining Eurasian species not illustrated in Fibiger and Hacker (2007) in the literature (Hampson 1908; Draudt 1950) shows that two additional species are likely part of the *paleacea* / Nearctic group, namely *E. kansuensis* Draudt, 1935 and *E. fuliginosa* Draudt, 1950, both described from China. The description and type illustration of *E. fuliginosa* is quite similar to *E. infumata*, and genitalic comparison of the two may show they are closely related. Additional research is needed to fully evaluate the taxonomic status of the western U.S. *E. decolor* populations, and the enigmatic Pacific Northwest *E. fausta* populations.

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